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Ecosystem assembly rules: the interplay of green and brown webs during salt marsh succession

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Abstract. Current theories about vegetation succession and food web assembly are poorly compatible, as food webs are generally viewed to be static, and succession is usually analyzed without the inclusion of higher trophic levels. In this study we present results from a detailed analysis of ecosystem assembly rules over a chronosequence of 100 years of salt marsh succession. First, using 13 yearlong observations on vegetation and soil parameters in different successional stages, we show that the space-for-time substitution is valid for this chronosequence. We then quantify biomass changes for all dominant invertebrate and vertebrate species across all main trophic groups of plants and animals. All invertebrate and vertebrate species were assigned to a trophic group according to feeding preference, and changes in trophic group abundance were quantified for seven different successional stages of the ecosystem. We found changes from a marine-fueled, decomposer-based (brown) food web in early stages to a more terrestrial, plant-based, herbivore-driven (green) food web in intermediate succession stages, and finally to a decomposer-based, terrestrial-driven food web in the latest stages. These changes were accompanied not only by an increase in live plant biomass and a leveling toward late succession but also by a constant increase in the amount of dead plant biomass over succession. Our results show that the structure and dynamics of salt marsh food webs cannot be understood except in light of vegetation succession, and vice versa.

Key words: chronosequence; detritivore; ecosystem assembly rules; food web; herbivore; salt marsh; Schiermonnikoog, The Netherlands; succession.

Introduction

One of the central issues in ecology is how ecological forces shape communities of species that interact across multiple trophic levels. Studies of vegetation succession and food web assembly have generated many insights on this topic. Although quite separate, vegetation succession has generally been viewed as a linked plant- and soil-driven process in which the focus is on plant colonization, facilitation (soil modification), and interspecific competition/exclusion among plant species as driving forces, all within this one trophic level (Clements 1916, Miles and Walton 1993). More recently, this is combined with research on plant traits into the study of community assembly rules. Compositional changes in connected trophic levels (herbivores, predators, decomposers) in such successional ecosystems have long been assumed to be the derivative of such plant-driven succession (Connell and Slatyer 1977). Food web ecologists, on the other hand, have mostly viewed communities as static entities in which plants are just one of the trophic levels, and the interplay among trophic levels sets the equilibrium community composition of each (Schoener 1983, de Ruiter et al. 1995, Berlow et al. 2004, Moore et al. 2004, Rooney et al. 2008). This means that current theories of vegetation succession and food web assembly are poorly compatible, which calls for studies that better integrate food web structure with the dynamics of vegetation succession (Schmitz et al. 2006). This requires new insights into how entire ecosystems assemble over time, not only communities at specific trophic levels.

Several authors have raised objections to the strongly plant-centered view of community assembly and succession (Odum 1969, Connell and Slatyer 1977) and have argued for a more integrative approach that explicitly takes plants and higher trophic levels from both the "green web" (herbivore-based, with abundant predators of herbivores) and "brown web" (detritivore-based, with abundant predators of detritivores) into account (Connell and Slatyer 1977, Moore et al. 2004, De Deyn and Van der Putten 2005). Initial studies on multitrophic community organization along gradients of primary productivity predict that herbivore densities first increase, with more plant productivity and control plant standing biomass at the same level (green web interactions), until predation (Oksanen et al. 1981) or plant quality (Van de Koppel et al. 1996) limit further growth

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of the herbivore population. Other studies have focused more on the interactions between plants, organic matter production, and decomposer densities (brown web interactions; Berendse et al. 1994, Moore et al. 2004, Wardle et al. 2004, Berg and Bengtsson 2007). However, in some of the most intensively studied successions, plants were found to play a minor role in the first stages of succession (Edwards and Sugg 1993, Kaufmann 2001, Hodkinson et al. 2004) or were not even present at all (Payne 1965, Polis and Hurd 1995, Hodkinson et al. 2001). This raises general questions about the extent to which the green and the brown food webs determine the onset and outcome of succession and how the importance of these food web components changes over the course of primary succession.

The challenge, then, is to show how the interplay between vegetation succession and food web ecology leads to ecosystem assembly over time. In particular, can we identify "ecosystem assembly rules" based on variation in average traits among trophic groups that govern ecosystem development over time? Thereby, we expand on the current agenda of "community assembly rules," which are based on variation in traits among species *within* trophic groups (Levin et al. 2001, Mutshinda et al. 2009). As mentioned, many have stressed the importance of the interactions between detritivores and herbivores in shaping the trophic structure of ecosystems, but how both the brown web (detritivore-based, sensu Moore et al. 2004) and the green web (herbivore-based) interact over succession is still poorly understood. This requires an integrated approach in which the temporal component is also taken into account (Bardgett et al. 2005). As the long-term dynamics in this type of long-term ecosystem assembly are poorly known, good descriptions in validated chronosequences are needed first. These can then form the basis for theoretical and experimental work to further explain the observed patterns.

Ecosystems can persist in alternative food web configurations, characterized by the number and identities of important pools and fluxes, their relative sizes, and the connections among them (Shurin et al. 2006). In Fig. 1 we suggest four typical food web configurations that may be observed both in different ecosystems and in different successional stages of the same ecosystem. The first theoretically possible configuration (Fig. 1A) is dominated by the brown web and thrives on input of organic material (S), as observed in coastal desert by Polis and Strong (1996). The second possible state (Fig. 1B) is characterized by a self-sustaining, small green web and a small detritus pool with high turnover and low inputs, as observed in early stages of sand dune succession by Olff et al. (1993), for example. The third state (Fig. 1C) can be characterized by green and brown webs that are both well developed, and which "compete" with each other for the available nutrients, as observed in grazing ecosystems (Cebrian and Lartigue 2004), for example. A small external input or subsidy as well as a small internal output of material is often present in this state. The last state (Fig. 1D) is fundamentally different from Fig. 1A as it is characterized as a large, but low-quality plant production (high C:N ratio), which leads to a small green web and a large brown web, as observed in boreal forests (Hilli et al. 2010), for example. In such situations, decomposition by fungi and bacteria of dead plant material is essential to facilitate higher trophic levels (macrodetritivores and their predators), as the quality of the undecomposed plant material is insufficient to support most herbivores. Not only may these different configurations represent different types of ecosystems, but we also propose that they can represent different stages of ecosystem succession, thus revealing processes of ecosystem assembly.

In this study, a thorough documentation of the long-term succession of a salt marsh food web is presented as a first step in this research agenda on ecosystem assembly rules, which links succession and food web structure, with equal attention to its green and brown parts, resulting in such ecosystem assembly rules. We chose a salt marsh ecosystem for this study because this habitat is characterized by a limited number of species that are all able to cope with the generic physical and chemical stress factors (like flooding, salinity, waterlogging, anaerobic conditions, H_2S toxicity). We performed a complete analysis of the dynamics of all main trophic groups of both the green and brown web along a 100 year-old salt marsh chronosequence. First, we quantified the biomass for each group in seven different successional stages. Second, we related the observed ecosystem assembly to the main environmental changes during succession.

We finish by providing future directions in the analysis of ecosystem assembly rules and the consequences they may have for general understanding of how lots of things are put together in ecosystems, i.e., when organisms both modify their environment and interact within and across trophic levels and among the green and brown parts of food webs (sensu Olff et al. 2009).

Methods

Description of salt marsh chronosequence

Measurements on ecosystem assembly of food web composition were performed on the salt marsh of the island of Schiermonnikoog (53°30′ N, 6°10′ E), The Netherlands, in July 2008. The yearly temperature on the island is 10.2° ± 0.72°C (mean ± SD), and rainfall is 824 ±149.1 mm (data *available online*).[4] On the salt marsh of Schiermonnikoog a chronosequence is present that spans 100 years of succession (Olff et al. 1997). The earliest stages are formed on the east side of the island; late-succession stages are situated 8 km to the west.

[4] Data are from the Royal Netherlands Meteorological Institute at www.knmi.nl

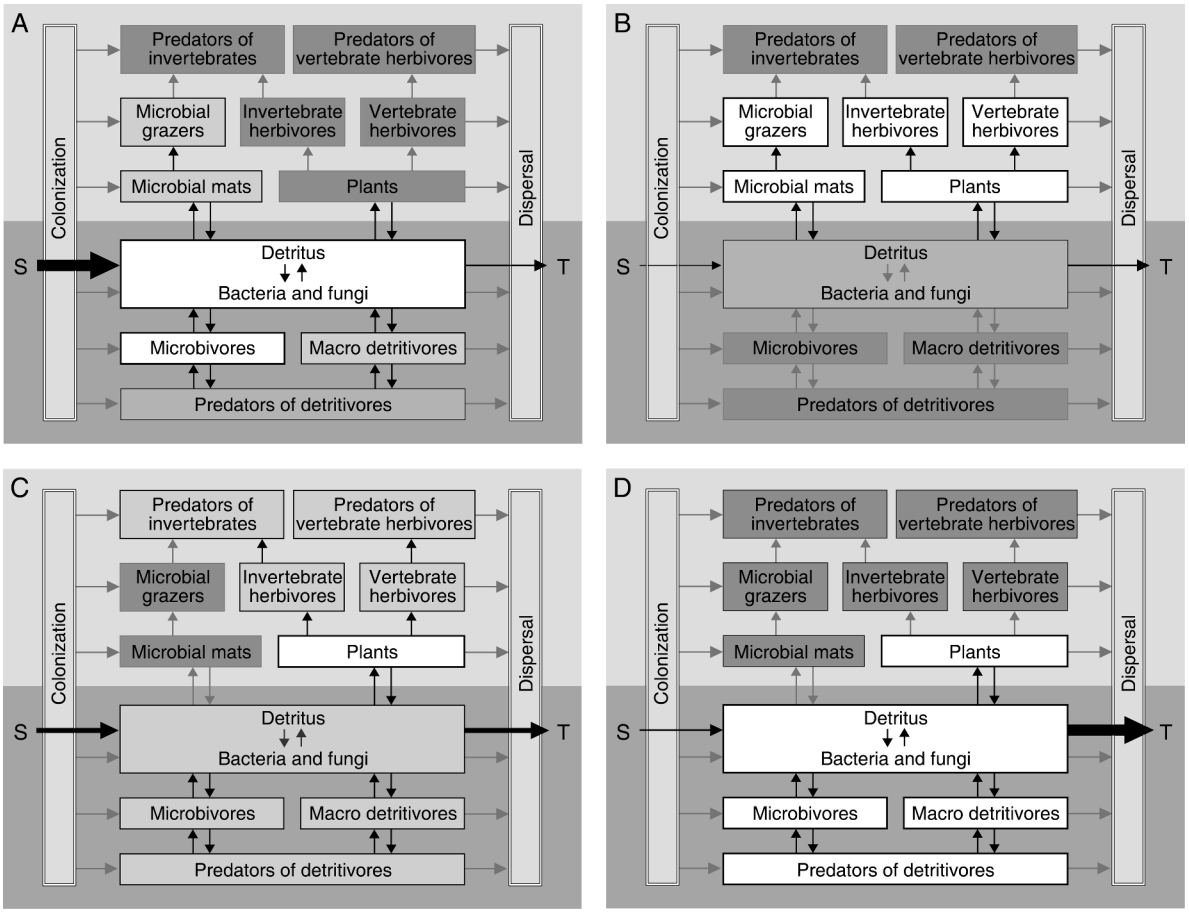

FIG. 1. Alternative main food web configurations between ecosystems, or successional stages within an ecosystem, with the differences between configurations determined by the number and identities of important pools and fluxes, and their relative sizes. The upper seven compartments within each subfigure represent the green web (terrestrial, plant-based, herbivore-driven), while the lower five compartments represent the brown web (marine-fueled, detritivore-based food web in early stages). Food web compartments with a higher biomass and flux are indicated with a lighter shade. During primary succession, either configuration (A or B) can be a precursor for (C), after which panel (D) represents the last stage. In configuration (A), primary production is very low but with a high external input of dead organic matter, S, depicted as a thick arrow pointing into the box Detritus. As a result, the brown web dominates the food web. Exports, T, from the ecosystem are very small, depicted by the thin arrow pointing out of the box Detritus. Succession state (B) consists mostly of a green web, which is based on nutrients and energy locally captured by the vegetation. Imports and exports of organic matter from the ecosystem are small. In configuration (C), both abundant green and brown webs occur, in which all trophic groups are common, and which mostly rely on locally produced primary production. In configuration (D), the majority of energy and nutrients produced by plants is used by the brown web, with a sizable amount of organic matter exported.

During succession, vegetation composition changes from a state with very sparse vegetation toward a species-rich vegetation in intermediate succession stages and a tallgrass monoculture in late-succession stages (Olff et al. 1997). The justification of the space-for-time replacement of this succession was checked by monitoring permanent plots in different successional stages during the last 13 years. At locations of successional age 0, 14, 27, 37, 60, and 85 years (age in 1994; Olff et al. 1997), biotic and abiotic parameters were collected over a 13-year period. At 12 points in these six locations, we measured sediment layer depth (to the nearest 0.5 cm) and changes in cover of three dominant plant species: *Plantago maritima* (an early-successional species, highly preferred by geese; Stahl et al. 2006), *Artemisia maritima*, and *Elytrigia atherica* (species of the intermediate and late succession, respectively; Olff et al. 1997).

Sampling design

Seven successional stages were identified, estimated as 0, 10, 25, 35, 45, 55, and 100 years of developmental age in 2008 (Appendix A; see Plate 1). More information on vegetation composition in the different successional stages can be found in Appendix B: Table B1. Salt marsh age at each successional stage was estimated from topographic maps, aerial photographs, and the thickness of the sediment layer accumulated on top of the underlying sand layer (Olff et al. 1997). The sites were

selected to have a similar base elevation (position at the initial elevation gradient on the bare sand flats with a base elevation of 1.16 m ± 2.2 cm [mean ± SE] above Dutch Ordinance Level). Different base elevations will have different inundation regimes, and therefore each has its characteristic vegetation succession (Olff et al. 1997). As salt marsh matures, sediment trapping by the vegetation at this base elevation increases the elevation of the soil surface with ~16 cm of clay in addition to the base elevation over 100 years of salt marsh succession, reducing the inundation frequency by floods, such as during spring tide.

Five sampling points within each of the seven successional stages were used. At these 35 sampling points, five different collection/sampling techniques were used to characterize the different components of the above- and belowground food web. Enclosed pitfall traps (diameter 10 cm in 50 × 50 cm Perspex enclosures) were used to gain quantitative estimates on soil-inhabiting invertebrates such as snails, spiders, beetles, and beach hoppers. This method is especially suitable to estimate abundances of surface-active species and was adapted after Lang (2000). The combination of the long sampling period (18 days) and the small sampling area ensured that there was no bias toward the more active species, which is a fundamental problem of nonenclosed pitfalls (Lang 2000). A more elaborate description and a picture of this method are given in Appendix D: Fig. D1A. Closed insect-emergence traps of 50 × 50 cm and 80 cm height were used to collect flying insects emerging from the soil and vegetation (Ausden 2000). An illustration of this method is provided in Appendix D: Fig. D1B. These two methods were used in the period 4–22 July 2008 and traps were emptied every third day in order to completely "empty" the plot. Accumulation curves for common species indeed showed a strong leveling off toward the end of this period (including the land snail species *Ovatella myositis*), suggesting that the time of sampling was sufficient to catch most specimens (see Appendix E: Fig. E1). For both surface-active species (Appendix E: Fig. E2A, B) and for flying invertebrates (Appendix E: Fig. E2C–E), more shaded, later-successional sites did not have a lower accumulation of individuals (the exponent of the line) than the early successional (fully exposed) sites. This indicates that there is no strong effect of differences in soil temperature on the catching rate of similar species in our study area.

Soil macro- and larger mesofauna (e.g., springtails, oribatid mites, enchytraeid worms) were extracted from soil cores (diameter 10 cm, 5 cm height) using a Tullgren funnel extraction method (Van Straalen and Rijninks 1982). Nematodes were not sampled.

Hare and goose densities were estimated every two weeks during 1–14 May and 1–15 July 2008 by averaging pellet counts of accumulated droppings (Kuijper and Bakker 2005, Stahl et al. 2006).

Plant biomass was estimated by clipping the vegetation in 50 × 50 cm squares, to 1 cm height. Living and dead portions of plant biomass were carefully separated and afterward dried at 70°C for 48 h. To account for attached clay and sand, ash-free dry mass was determined as loss on ignition at 550°C for 3 h (Van Wijnen and Bakker 1999). Vegetation height was determined three times, 2 m apart, at each of the sampling points, using a 20-g drop disc. Soil temperature was measured continuously, using iButtons (Maxim, San Jose, California, USA). Soil moisture was measured using a ThetaProbe moisture meter (Delta-T Devices, Cambridge, UK) twice during the measuring period. In order to characterize external (marine) input, biomass of macroalgal driftline material (mainly *Fucus* spp.) was estimated during April, May, and June 2009, inside a 5 × 5 m square at each of the 35 sampling points. A clay core was used to determine the increase in sediment depth over succession (to the nearest 0.5 cm).

Biomass calculations and feeding guilds

Invertebrates were identified up to species level and afterward merged into feeding groups according to the classification in Appendix C (Table C1), using feeding preferences for each species of invertebrate according to Remmert (1983), Irmler and Heydemann (1986), Berg et al. (2004), Caballero et al. (2004), and Krantz and Walter (2009). The biomass for each species at each successional stage was estimated using the species-specific number to biomass corrections of Petersen and Luxton (1982), Caballero et al. (2004), Krantz and Walter (2009), and our own measurements (for details, see Appendix C: Table C1). For some of the dominant species, namely, *Orchestia gammarellus* (macrodetritivores; Amphipoda), *Fucellia maritima* (macrodetritivores; Diptera), *Ovatella myosotis* (algal feeders; Gastropoda), and *Pardosa purbeckensis* (aboveground predators; Aranea), the density to biomass conversion was determined experimentally by calculating dry mass from 200 randomly selected individuals.

Hares are estimated to produce about 400 droppings per day (estimated allometrically from rabbit dropping count of Lockley 1962), while geese produce about 200 pellets per day (Bazely and Jefferies 1985). Dropping counts are commonly regarded as good indicators of grazing activity for both geese (Owen 1971) and hare (Langbein et al. 1999).

In the results, we presented metabolic mass instead of biomass for all animals, but not for plants. Metabolic mass is calculated as biomass$^{(3/4)}$ (Kleiber 1947) and corrects for the fact that small animals have a higher metabolic rate per gram body mass than larger organisms, so the importance to the ecosystem also scales with that (Peters 1986).

Results

The thickness of the sediment layer at the permanent plots increased predictably with time (Fig. 2A), both

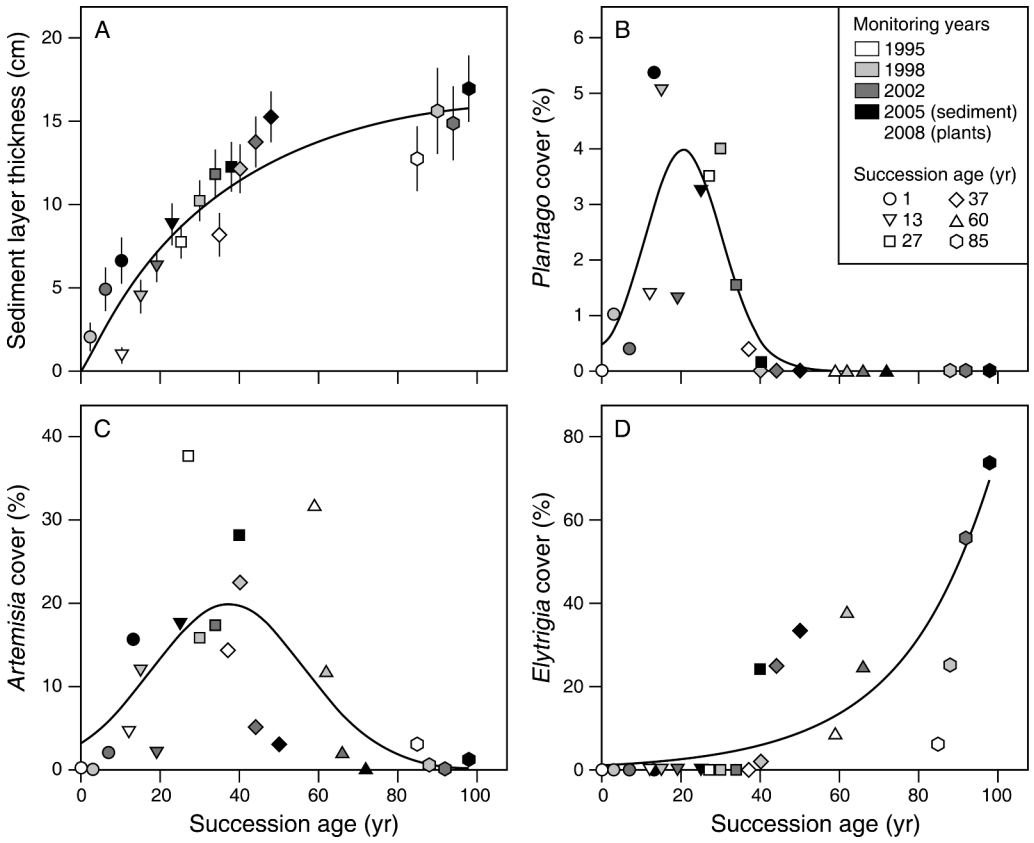

FIG. 2. Illustrations of the space-for-time substitution for the 100-year chronosequence on the salt marsh of Schiermonnikoog, The Netherlands. (A) Increase in the sediment layer (exponential rise to maximum, $R^2 = 0.86$; $P < 0.0001$). Error bars represent SD in clay layer thickness of 12 points (the same 12 points at the same base altitude near the same vegetation plot). (B) Cover of *Plantago maritima* (Gauss, $R^2 = 0.65$; $P < 0.001$). (C) Cover of *Artemisia maritima* (Gauss, $R^2 = 0.39$; $P < 0.001$). (D) Cover of *Elytrigia atherica* (exponential increase, $R^2 = 0.73$; $P < 0.001$). Sediment layer measurements were done in 1995, 1998, 2002, and 2005, and vegetation cover was determined in 1995, 1998, 2002, and 2008. Different shadings of gray indicate the years in which the measurements were done.

within and between locations. Along the same successional time axis, dominant plant species showed predictable changes in cover (Fig. 2B–D). *Plantago maritima* showed a pronounced peak after 20 years of succession (Fig. 2B). *Artemisia maritima* showed a peak at intermediate succession (40 years; Fig. 2C), while the late-successional dominant species *Elytrigia atherica* started to increase only after 40 years of vegetation succession (Fig. 2D) and became dominant at 100 years. These patterns were reflected at each of the individual permanent plots, which indicates that our successional sequence is indeed a proper space-for-time substitution.

In the earliest stage of salt marsh succession (0 years), we found every trophic group from Fig. 1 except invertebrate herbivores (Fig. 3A–I). We observed low plant biomass, covering only 8% ± 3% (mean ± SE) of the soil (Appendix B: Table B1). Total dry biomass of organisms relative to total plant biomass (live plus dead) in the earliest stage of succession was 14.6% ± 3%. This was 5–16 times higher than in any of the other succession stages between 10 and 100 years, which ranged between 0.89% and 3% (mean 1.86% ± 0.7%). This indicates that other sources of organic matter may support the food web as well, and/or the turnover of the plant biomass is very high. Green web biomass formed by predators of herbivores and herbivores of plants was low in the earliest stage of succession (Fig. 3A–F) and consisted mainly of biomass of herbivorous vertebrates (Fig. 3C, D). Algae-consuming invertebrates were present with low biomass (Fig. 3F). Microbivores (Fig. 3H) and belowground predators (Fig. 3I) were already present in the earliest stage of succession, with densities comparable to those of aboveground predators. A species of Diptera, *Fucellia maritima*, and to a lesser extent Enchytraeidae spp., made up the majority of the macrodetritivore biomass in this early succession (Fig. 3H). The first species is known to occur predominantly in decaying algae (Remmert 1983), and the second species also was found under decaying algae (M. Schrama, *personal observation*).

An increase in the biomass of the trophic groups in the green web was observed between the youngest stage

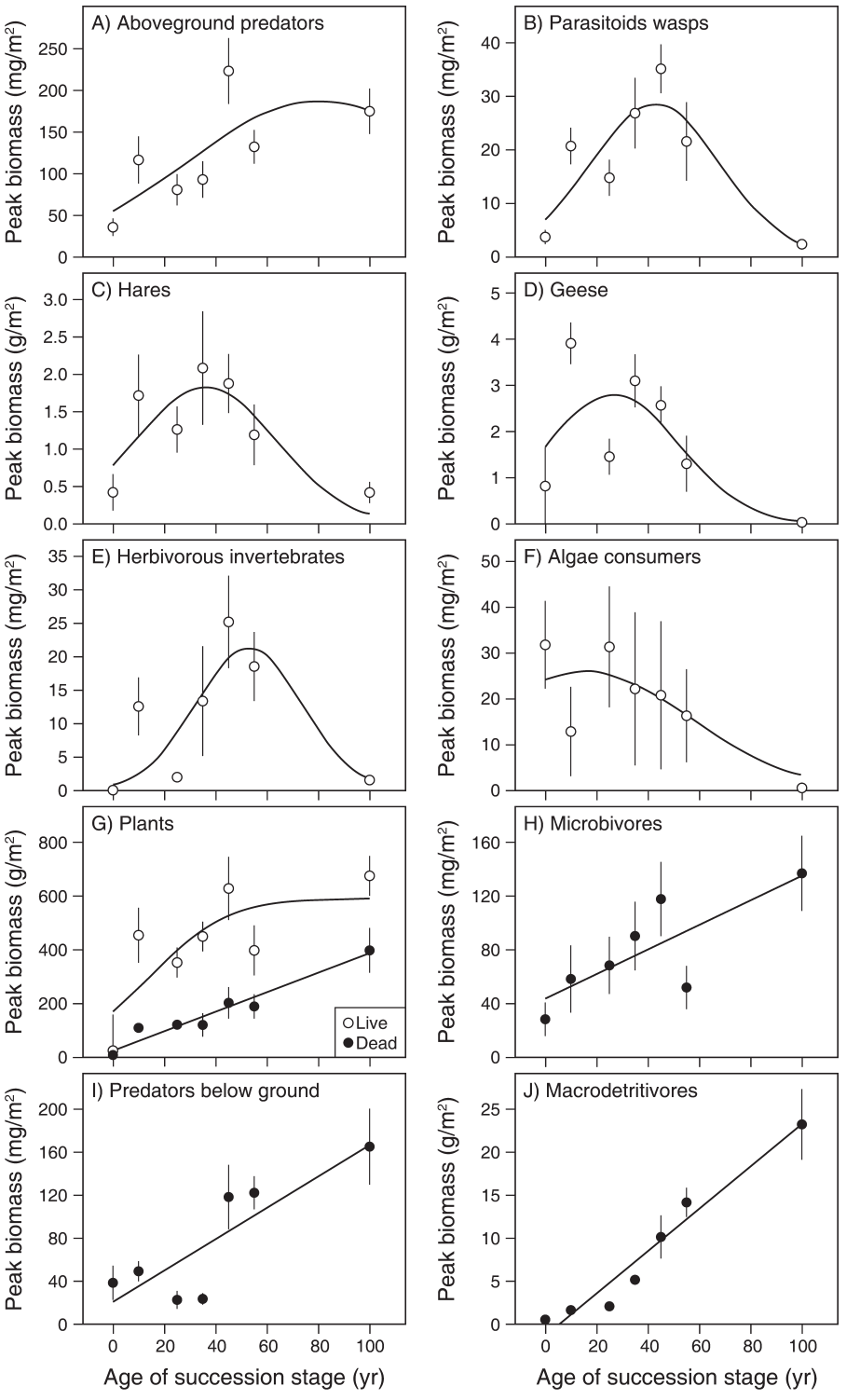

FIG. 3. Peak biomass (mean ± SE) of dominant trophic groups along the successional chronosequence (age of marsh). Fits indicate significant correlations. The green (herbivore-based) part of the food web is shown in open circles; the brown (detritivore-based) part of the web is indicated by solid circles. (A) Aboveground predators (Gauss, $R^2 = 0.46$; $P < 0.001$). (B) Parasitoid wasps (Gauss, $R^2 = 0.46$; $P < 0.001$). (C) Hare (Gauss, $R^2 = 0.19$; $P = 0.014$). (D) Geese (Gauss, $R^2 = 0.27$; $P = 0.003$). (E) Herbivorous invertebrates (Gauss, $R^2 = 0.19$; $P = 0.014$). (F) Algae consumers (Gauss, $R^2 = 0.27$; $P = 0.002$). (G) Live (power, $R^2 = 0.51$; $P < 0.001$) and dead standing aboveground biomass (linear, $R^2 = 0.78$; $P < 0.001$). (H) Microbivores (linear, $R^2 = 0.24$; $P = 0.002$). (I) Predators below ground (linear, $R^2 = 0.48$; $P < 0.001$). (J) Macrodetritivores (linear, $R^2 = 0.78$; $P < 0.001$).

(0 years) and the intermediate stage of succession (45 years; Fig. 3A–F). Invertebrate herbivores reached their highest biomass in stage 45 years of succession (Fig. 3E). Parasitoid wasps, which predate on aboveground species (Quicke 1997), also showed a clear biomass optimum in intermediate succession, at 45 years (Fig. 3B). Vertebrate herbivore biomass for geese and hare both showed a clear biomass optimum at succession stage 35 and 45 years, respectively (Fig. 3D, C). Vegetation biomass change between early and intermediate succession was characterized by a strong increase in aboveground standing biomass (Fig. 3G), where aboveground standing live biomass increased stronger than standing dead biomass (an increase of 584g/m^2 for live biomass vs. an increase of 198g/m^2 for dead biomass [Fig. 3G]).

We also observed a clear, continuous increase in the biomass of brown web trophic groups between early (0 years) and intermediate succession (45 years; Fig. 3H–J), although less strong than the increase in the biomass of green web groups (Fig. 3A–F). The most abundant species in the brown web at intermediate successional stages, *Orchestia gammarellus,* replaces *Fucellia maritima* between 10 and 25 years as the macrodetritivore species with the highest biomass, increasing to up to 90% of the invertebrate biomass in the final successional stage.

From intermediate (45 years) to late succession (100 years), live vegetation biomass did not increase, while standing dead biomass seemed to show a steady increase toward late succession (Fig. 3G). Biomass of first-order consumers in the green web biomass showed a sharp decline toward late succession (Fig. 3C–E) for both vertebrates and invertebrates, while the biomass of first-order consumers in the brown web showed a pronounced increase toward late succession (Fig. 3H–J). The fraction of the total biomass of invertebrate primary consumers that was taken by herbivorous invertebrate herbivores also showed a pronounced peak between early and intermediate succession (Fig. 4). Biomass of invertebrate primary consumers in the brown web showed the opposite pattern, with relatively high biomass in early and late succession. Second-order green web consumers mirrored these patterns (Fig. 3B, I), except for aboveground predators (Fig. 3A), which did not decrease toward late succession but rather seemed to level off.

Changes in important environmental factors

Over the succession gradient, many environmental and abiotic properties change (Fig. 5). We found a clear saturating decrease in the amount of bare soil (Fig. 5A). Furthermore, we found an increase in the sediment layer thickness over succession (Fig. 5B), which reflects a similar increase in the availability and pool of soil nutrients in the system (Olff et al. 1997), and a decrease in inundation frequency (Fig. 5G). The input of macroalgae in the early stages of succession is much higher than in the older stages (Fig. 5C). Vegetation height

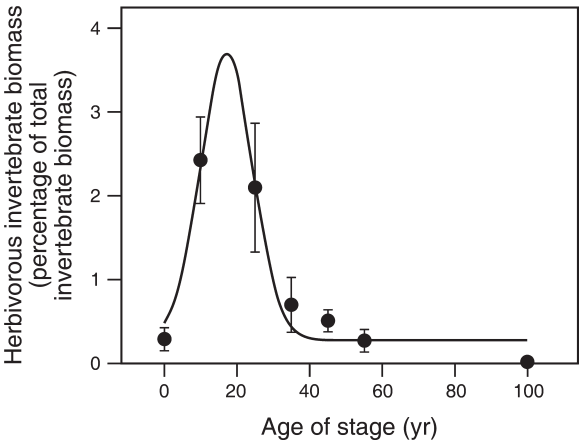

FIG. 4. Biomass of herbivorous invertebrates (mean ± SE) along the chronosequence as a percentage of the total invertebrate biomass (Gauss, $R^2 = 0.57$; $P < 0.001$).

starts below 1 cm in the first stage of succession, but increases up to 26 cm toward the last successional stage (Fig. 5E). Soil surface temperatures (Fig. 5E) and also temperature fluctuations are highest in early, barely vegetated stages and show a mean decrease of 4°C toward the late-successional stage. Soil moisture decreases over succession (Fig. 5F), but we found a much lower value for the earliest stage of succession where the clay layer is absent.

DISCUSSION

Our results suggest that the first successional stage is dominated by external detritus inputs, thus resembling food web configuration A in Fig. 1. This is different from the classic view of early primary succession dominated by colonizing plants as depicted in configuration B. Over succession, we found the food web configuration to change toward configuration C, with an increasingly abundant green web but still a sizeable brown web. Toward the late stages of succession, the brown web became again overwhelmingly abundant, with high plant biomass that is hardly used by herbivores, corresponding to configuration D in Fig. 1.

We expect that our sampling methods appropriately captured the changes in main food web configuration during this succession sequence. As the growing season on the salt marsh is relatively short, plant and animal biomass and activity show a pronounced peak in July (Irmler and Heydemann 1986). We expect that sampling in more seasons would not affect our conclusions. In addition, it should be noted that the use of biomass of trophic groups has limitations in quantifying food web structure, as it does not fully capture the interaction strength between groups. For instance, trophic groups with high turnover rates may contribute more strongly to trophic dynamics than expected from their biomass. Also, nontrophic (e.g., perceived predation risk) interactions are not captured in the estimated biomass.

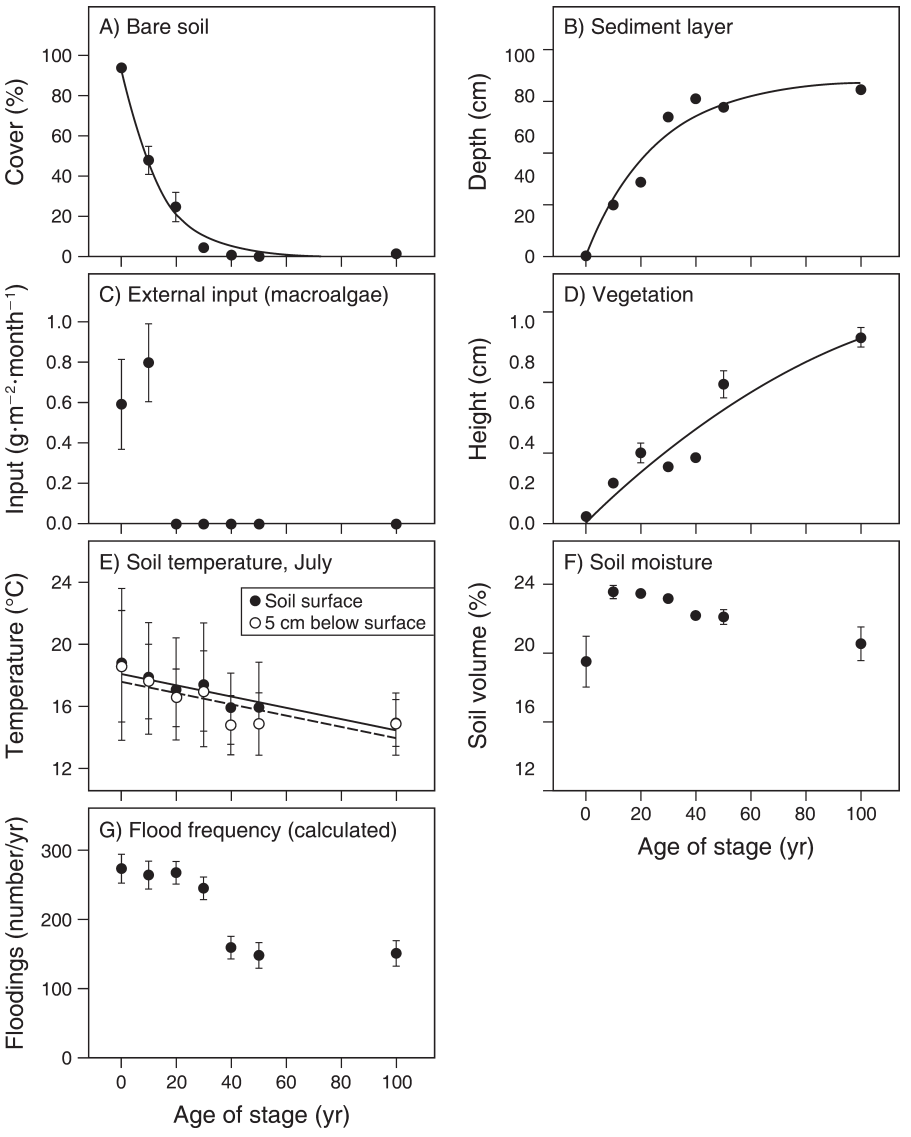

FIG. 5. Changes in environmental and abiotic parameters (mean ± SE) over the chronosequence. Fits indicate significant correlations. (A) The percentage of bare soil decreases strongly with age of succession. (exponential decrease, $R^2 = 0.89$; $P < 0.001$). (B) Sediment layer increases in depth with succession to ~16 cm thick (exponential rise to maximum, $R^2 = 0.88$; $P < 0.001$). (C) External input of macroalgae is present only in the first stages of succession. (D) Vegetation height increases strongly toward late succession (exponential rise to maximum, $R^2 = 0.87$; $P = 0.002$). (E) Soil temperatures (mean ± SD) on the soil surface (linear, $R^2 = 0.81$; $P = 0.003$; solid circles) are, on average, 0.5°C higher than soil temperatures at 5 cm depth (linear, $R^2 = 0.57$; $P = 0.03$; open circles; general linear model, $F = 90.8$; $P < 0.002$). (F) Soil moisture as a percentage of soil volume first shows a strong increase and then a gradual decreasing trend toward late succession. (G) Flooding frequency decreases with increasing sediment layer thickness toward later stages of succession (elevation calculations after Olff et al. [1997]).

Nevertheless, we expect that our main conclusions also hold up during more detailed analysis of trophic dynamics in this ecosystem.

In Fig. 1 we propose that ecosystem assembly can either start as a green- or brown-dominated food web (Fig. 1A vs. B). The high biomass of the brown web in early succession, attended with low observed plant biomass, strongly suggests that the initial buildup of organic material in the earliest stages of this primary succession does not depend much on locally produced plant material. The dominant species that were caught in this stage have a stationary lifestyle (*Diptera* larvae and Enchytraeidae), which makes it unlikely that the high biomass of animals compared to the amount of primary producers can be explained by an oversampling of trespassers. The brown-web-dominated first stage of succession is therefore an example of a marine subsidy to a terrestrial ecosystem as first observed by Polis et al. (1997). Also, Boschker et al. (1999) showed that bacteria on the young salt marsh of Schiermonnikoog are mostly

PLATE 1. Experimental setup at the 35-year-old successional stage on the salt marsh of Schiermonnikoog, The Netherlands. Photo credit: M. Schrama.

dependent on marine inputs as an energy source. If this is correct, we would conclude that the food web configuration in Fig. 1A captures the start of this succession better than configuration B; or said otherwise, the succession is started up by the brown web, not by the green web.

Our results show that the next stage in succession can be characterized by the configuration in Fig. 1C, a food web that is mostly fueled by local primary production with a substantial green web. Between the stages of 10 and 45 years, we observed an increase in the importance of the green web relative to the brown web. This increase in herbivore biomass during succession is in line with classical exploitation theory (Hairston et al. 1960, Rosenzweig 1973, Oksanen et al. 1981, Van de Koppel et al. 1996). Increasing primary production of high quality, and thus more food, likely explains the increasing abundance of vertebrate herbivores over early succession. Previous work in this system has indicated that these vertebrate herbivores not only respond to but also affect the course of vegetation succession (Olff et al. 1997, Van Wijnen and Bakker 1999, Kuijper and Bakker 2005). As a consequence, vertebrate herbivores may strongly affect various groups of invertebrates in the intermediate stages of this succession (interactions within the green web).

From intermediate to late succession (from 45 to 100 years), we observed a shift from a mixed green/brown food web configuration (Fig. 1C) toward a configuration with high plant production, few herbivores, and dominance of the brown web (Fig. 1D). Although we base this conclusion only on the last three successional stages, our space-for-time justification shows that the 75-year-old stage is, at least regarding clay layer and vegetation composition, intermediate to the 55- and 100-year-old stages. The shift in food web configuration may be explained by a decrease in forage quality for herbivores during these stages in succession (Van der Wal et al. 2000*b*), caused by increased nutrient availability, primary productivity, and associated plant competition for light (Van de Koppel et al. 1996, Olff et al. 1997). In turn, this has led to dominance of plant species with high structural support and hence low palatability (Van der Wal et al. 2000*a*, Bos et al. 2005). In intermediate successional stages, small vertebrate herbivores still interact strongly with the course of succession by increasing forage quality (Kuijper and Bakker 2005), while in later stages, the ongoing vegetation succession causes herbivores to "lose control" over vegetation composition (Van der Wal et al. 2000*b*, Kuijper and Bakker 2005). As a result, macrodetritivores make up most of the animal biomass in late succession, with the terrestrial amphipod *Orchestia gammarellus* as a dominant species, comprising ~90% of the total faunal biomass. The dominance of this species is a common phenomenon on mature productive salt marshes (Dias and Sprung 2003, Petillon et al. 2005). As *Orchestia gammarellus* produces large amounts of excrement on the surface (turnover of organic matter) and exhibits extensive digging behavior (improving soil aeration; Moore and Francis 1986, Dias and Sprung 2003), it can be expected to act strongly on nutrient cycling (Bardgett and Wardle 2010). We therefore speculate that this brown web dominance of

nutrient recycling is associated with late-successional, taller plant species, which in turn may promote macrodetritivores, while repelling herbivores.

Toward late succession, the biomass of aboveground predators declines less steeply than other aboveground trophic groups, such as parasitoid wasps and invertebrate herbivores. This suggests that many of the ground-active species either do not feed specifically on green web prey or may change their diets along succession from green to brown web prey. This is supported by other studies that find predators to connect different compartments across green and brown webs (Berg et al. 2001, Schmitz 2007, Birkhofer et al. 2008), which has been suggested to stabilize food webs (Neutel et al. 2007). To what extent aboveground predatory species shift their diet from herbivorous to detritivorous species deserves further investigation.

A general pattern?

We are inclined to think that our observed succession of main food web configurations represents a general pattern of ecosystem assembly. Although salt stress and stress from waterlogging are critical determinants of the salt marsh ecosystem that prevent final succession into forest, we argue that the principles underlying the observed changes in food web configuration can also apply to other ecosystems. For example, decreasing vegetation quality (Van der Wal et al. 2000*b*) and increasing structural complexity (increasing amount of dead organic material and standing biomass, and increasing vegetation height) are typical for many successional sequences (Odum 1969). Therefore, the food web configuration in Fig. 1D is suggested to be the end stage for many ecosystems, including forest, a state with a relatively high C:N ratio of locally produced organic matter, a high standing stock of species belonging to the brown web, and a low biomass of species belonging to the green web. However, some terrestrial ecosystems, such as savannas, which are dominated by large grazers and/or fire, pose an obvious exception to this, as these agents prevent low-quality plant tissues to dominate ecosystem processes in these systems (McNaughton 1984, Holdo et al. 2009). If this is correct, the food web configuration in Fig. 1C is merely the end point of succession in these ecosystems. An interesting parallel to this can be found in salt marsh where large herbivores (cattle, horses) are introduced as grazers. They seem to shift the system back toward configuration C, with higher vegetation diversity, improvement of plant quality, and return of other (smaller) herbivores (Olff et al. 1997, Bos et al. 2002, Loucougaray et al. 2004).

Another critical difference between a salt marsh succession and other ecosystem successions arises from the amount of external nutrient input by sedimentation that governs the speed with which succession takes place (Olff et al. 1997). Due to the high external input and the short maturation time salt marsh plant species need, salt marshes are allowed to develop much faster than any forest will ever do. Mainland salt marshes, which receive up to 10 times higher organic input, develop much faster than the back-barrier island marsh that was investigated in the present study (Bakker et al. 2002). Succession goes much slower on primary successions like Glacier Bay (Crocker and Major 1955), Mount St. Helens (Sugg and Edwards 1998), and the retreating Rotmoos Glacier (Kaufmann 2001). The amount of nutrients that an ecosystem receives during its first stages of succession may be of critical importance to the question of whether succession will start with food web configuration A or B (see Fig. 1), and hence for the progress of further ecosystem assembly. In the examples with a slow rate of succession, low external input may force the ecosystem to accumulate nutrients by a slowly increasing primary production. In these ecosystems, typically configuration B is a much more appropriate start situation than configuration A.

Conclusion: ecosystem assembly as merger of succession and food web theory?

Ecological theory regarding succession has mostly focused on vegetation being the primary determinant that shapes the ecosystem. Our results show that in early stages with little vegetation, decomposers set the scene. This indicates that early successional development may not be driven by vegetation alone. During intermediate succession, when vertebrate herbivores are present in high numbers, herbivores seem to react strongly to the much higher biomass. Earlier experiments have already shown that these very same herbivores change the course of succession strongly but fail to halt it completely, and thus show a strong decline after intermediate successional stages (45 years; Van de Koppel et al. 1996, Kuijper and Bakker 2005). We conclude that vegetation succession can be understood only in light of food web dynamics, and vice versa.

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Supplemental Material

Appendix A

Pictures of each of the sites along the successional gradient, taken in the summer of July 2008 (*Ecological Archives* E093-222-A1).

Appendix B

A table showing cover for the different plant species, total vegetation cover, and total number of plant species for all sites along the successional gradient (*Ecological Archives* E093-222-A2).

Appendix C

A table showing the species-specific mass, metabolic mass, and feeding group of all animals that were caught in all plots along the succession gradient (*Ecological Archives* E093-222-A3).

Appendix D

Pictures and explanation of trapping techniques (*Ecological Archives* E093-222-A4).

Appendix E

Figures showing the accumulation curves of trapped invertebrates for a number of dominant species, using the different trapping methods (*Ecological Archives* E093-222-A5).